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Behavioral and neuroimaging evidence

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Fluent readers recognize visual words across changes in case and retinal location, while maintaining a high sensitivity to the arrangement of letters. To evaluate the automaticity and functional anatomy of invariant word recognition, we measured brain activity during subliminal masked priming. By preceding targets words with an unrelated prime, a repeated prime, or an anagram made of the same letters, we separated letter-level and whole-word codes. By changing the case and the retinal location of primes and targets, we evaluated the invariance of those codes. Our results indicate that an invariant binding of letters into words is achieved unconsciously through a series of increasingly invariant stages in the left occipito-temporal pathway.

Considerable machinery lies behind the seemingly simple feat of word recognition (Posner & McCandliss, 1993). First, words must be recognized in spite of changes in font, size and retinal location. Second, letters must be bound together in a specific order, because different words can be written with the same letters. The present research had two aims: first, to clarify the cerebral stages of processing that lead to invariant word recognition, and second, to examine whether those stages can proceed in the absence of consciousness.

In literate adults, an extended strip of the left fusiform gyrus activates whenever visual words are presented (Cohen et al., 2000; Cohen et al., 2002; Nobre, Allison, & McCarthy, 1994). This region, which has been termed the Visual Word Form Area (VWFA), is responsive only to written words, not to spoken words (Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002). Its lesioning results in a severe word identification impairment, pure alexia, which is restricted to the visual modality (Leff et al., 2001). Thus, it is a plausible candidate for the neural basis of invariant visual word recognition.

To further specify the nature of word coding in the VWFA, we used the priming method (Grill-Spector & Malach, 2001; Naccache & Dehaene, 2001). Using an fMRI version of the masked priming paradigm (Forster & Davis, 1984), we previously observed that, when the same visual word is presented twice, first as a subliminal prime and then as a visible target, less activation is observed in the VWFA than when two different words are presented (Dehaene et al., 2001). A possible interpretation of this finding, based on single-cell studies in monkeys (Miller, Li, & Desimone, 1991), is that a population of neurons has been partially habituated by the presentation of the initial subliminal prime, and does not react as much when the same word appears as target.

By varying the degree of similarity between prime and target, one can then evaluate the selectivity of the coding of words. In our previous work, we observed that priming in the VWFA occurred even when there was a change of case between the prime and the target (e.g.

prime RADIO, target radio). This suggests that this area achieves case invariance (Dehaene et al., 2001). Here, we extend this work by examining whether the VWFA abstracts away from retinal features of the visual stimulus, and responds to single letters or to larger units.

Experiment 1 searched for regions with genuine case-invariant recognition. Most letters have similar shapes in upper and lower case (e.g. O-o). Thus, cross-case repetition priming effect might be explained by a generic capacity for size-invariant shape recognition, without implying a specialization for word recognition. However, some letters, such as A and a, have so radically different shapes in upper and lowercase that their correspondence is essentially arbitrary (Posner & Mitchell, 1967). Experiment 1 tested whether cross-case repetition priming occurred for words composed exclusively of such letters (e.g. RAGE-rage). Only regions genuinely engaged in case-invariant word recognition should be able to detect the identity of upper and lowercase words written solely with visually dissimilar letters (Bowers, Vigliocco, & Haan, 1998; Humphreys, Evett, & Quinlan, 1990).

In experiment 2, we then studied whether priming in those regions depends on the presence of individual letters or of larger constituents. This was achieved using "circular anagrams", pairs of words that can be transformed into each other by moving a single letter from front to back (e.g. range-anger; emit-mite). By priming a French word such as **reflet** ("mirror image") with its anagram **TREFLE** ("clubs"), we could repeat almost all of the same letters while presenting two unrelated words. By shifting the prime by one letter relative to the target, it was even possible to repeat almost all letters at the same retinal location, still without presenting the same word. If the VWFA is sensitive only to a word's component letters, it should show priming whenever letters are repeated, whether or not they compose a different word. This would fit with the hypothesis that only fragments of words can be extracted under conditions of subliminal presentation (Abrams & Greenwald, 2000). If, however, a whole-word code can be extracted subliminally, then we would expect greater priming when a word

is repeated than when it is preceded by its anagram. If such whole-word repetition effects survives a shift in the position of individual letters, it would further demonstrate that the neural code in the VWFA is capable of some degree of spatial invariance.

Method

Participants. 26 right-handed native French speakers participated (experiment 1: 2 men and 8 women, average 24 years; experiment 2: 5 men and 11 women, average 22 years). All subjects gave written informed consent. The study was approved by the regional ethical committee for biomedical research.

Procedure for experiment 1. Fourteen words were made of letters whose shape is similar in upper and lower case (Cc, Ff, Kk, Oo, Pp, Uu, Vv) and fourteen were made of dissimilar letters (Aa, Ee, Gg, Rr, Tt). They were matched in length (3-4 letters; means 3.36 and 3.43, $t(26)=0.37$) and frequency (means $\log_{10}$ frequency 1.26 and 1.10, $t(26)=0.39$). All were monosyllabic. On each trial, a sequence of fixation point, mask, prime, mask and target was presented as in Dehaene et al. (2001) (figure 1). The prime and target words always appeared in a different case, randomized across trials. Because of the small number of available words, it was not possible to use a classical task such as semantic classification. Rather, participants classified targets into those containing the letters A or E, and those containing the letters O or U. On non-repeated trials, the prime was a word of the same length drawn randomly from the other set of words, ensuring that the prime and target did not share a single letter.

The event-related fMRI protocol comprised 5 randomly intermixed event types. Four trial types were defined by the 2 x 2 combination of two factors, prime-target relation (same or different words) and letter similarity (target from the "similar" or "dissimilar" set). In a fifth trial type (baseline), only the masks were presented, and participants were told to rest for a few seconds. Trials were presented at a 2.4 s interval in 4 runs of 150 trials (30 of each type).

Procedure for experiment 2. Twenty pairs of circular anagrams appeared as both primes and targets (e.g. the French words TREFLE and REFLET; 4-6 letters, mean 4.83; 1-3 syllables, mean 1.73; mean $\log_{10}$ frequency 0.66). This restricted set of target words precluded using the same task as in experiment 1. Rather, participants classified the target words into bisyllabic words versus other words (with 1 or 3 syllables).

The fMRI protocol comprised 6 randomly intermixed event types defined by factors of prime-target relation and relative location (plus the same baseline condition as in experiment 1). First, primes and targets could be the same word (SW), or two anagrams (AN), or two different words (DW). Second, primes and targets could be presented at the same location (SL) or shifted by one letter (different location or DL; see figure 2). In each of 4 fMRI runs, 180 trials were presented, defining 6 conditions for fMRI analysis (C1 = 30 SW-SL words, C2= 30 SW-DL, C3 = 30 AN-SL, C4 = 30 AN-DL, C5 = 15 DW-SL + 15 DW-DL, and C6 = 30 baseline trials).

Assessment of prime visibility. After scanning, while still in the scanner, participants were told of the presence of primes and performed a 2-alternative forced-choice identification task. On each trial, a stimulus sequence identical to the main experiment was followed by a choice between two horizontally presented words. One word was identical to the prime, the other was unrelated and did not share any letter with the prime. Performance was at chance level (experiment 1: 53.8% correct, p=0.14; experiment 2: 51.4% correct, p=0.40), and participants denied seeing any primes.

Functional magnetic resonance imaging. We used a 3-Tesla whole body system (Bruker, Germany) and a gradient-echo echo-planar imaging sequence sensitive to brain oxygen-level dependent (BOLD) contrast (26 contiguous axial slices, 4.5 mm thickness; TR = 2.4 seconds). Data processing, performed with SPM99 software, included corrections for EPI distortion, slice acquisition time and motion; normalization; smoothing (8 mm); fitting with a

linear combination of functions derived by convolving a canonical hemodynamic response function and its time derivative with the known time series of the stimulus types; and random-effect group analysis. Effects of subliminal priming on BOLD activation were assessed within small regions of interest rather than using a whole-brain search. We first identified voxels involved in word processing in experiment 1 by contrasting word-present trials with baseline trials (voxel $p<0.01$, cluster-extent $p=0.05$ corrected across the brain volume). This initial contrast isolated 1155 voxels (bilateral occipital, supramarginal, central, precentral and cerebellar cortices as well as left fusiform and supplementary motor regions). Using the small volume correction of SPM, those voxels were then searched for significant priming effects. We examined the main effect of repetition (less activation to repeated than to unrepeated trials), the simple main effects of repetition restricted to similar or to dissimilar sets, and the conjunction of those two independent contrasts. In turn, the voxels that showed case-invariant priming in experiment 1 were used as a mask to constrain the search for priming effects in experiment 2. Because different subjects were used, this mask was smoothed at 8 mm. It was also symmetrized to avoid biasing the search towards the left hemisphere. In the end, 256 bilateral fusiform and parietal voxels derived from experiment 1 were searched for priming in experiment 2.

All comparisons reported in the table were tested at voxel $p<0.02$ and cluster-extent $p<0.05$ corrected for multiple comparisons across the small volume. Conjunctions were tested at voxel $p<0.01$ and were masked by the corresponding contrasts at $p<0.02$. Note that, given enough statistical power, subliminal priming effects reach significance in a whole-brain search and with the high thresholds conventionally used in fMRI. For instance, contrasting the different-case same-word and different-word conditions that were replicated in the present experiments 1 and 2 and in our earlier report (Dehaene et al., 2001), for a total of 36 subjects, subliminal priming was observed in a left fusiform cluster of 27 voxels (voxel $p<0.001$,

cluster-extent p=0.002, corrected for whole-brain search; peaks at -48, -48, -12, Z=4.55, and -44, -60, -8, Z=4.24).

Activations curves were obtained using a non-parametric regularized least square estimate of the event-related time course (Ciuciu et al., submitted). Percent signal change was then calculated by subtracting the mean peak activation, observed at 4.8 seconds following the stimulus, and the mean baseline activation value measured during a 4.8 second interval prior to stimulus presentation. Error bars indicate the between-subject standard error of the mean of each condition relative to the subject's grand mean.

Results

Invariance for case. Experiment 1 examined cross-case repetition priming for words made of letters with similar or different shape in upper and lower case (figure 1). Behaviorally, response times (RTs) were 23 ms faster for repeated words than for non-repeated words, $F(1,9)=33.9$, $p=0.0003$. There was no main effect of similarity ($p>0.93$) and no interaction of similarity and repetition ($p>0.14$). The repetition effect was significant with similar words (20 ms, $F(1,9)=18.4$, $p=0.002$) and with dissimilar words (26 ms, $F(1,9)=38.9$, $p=0.0002$). This replicates earlier results (Bowers et al., 1998; Humphreys et al., 1990), and indicates that a case-invariant representation, which has learned the arbitrary mapping between upper and lower case, was activated by the subliminal words.

In fMRI, reduced activation on repeated trials was seen in the left fusiform gyrus and, to a lesser extent, the right fusiform gyrus and the left parietal region (table 1). The large left fusiform cluster (antero-posterior coordinates -76 to -44 mm), most of which fell within the occipito-temporal sulcus at the border of the fusiform gyrus proper, replicated closely our earlier finding of case-independent priming (Dehaene et al., 2001). Conjunction analysis showed that the left fusiform, but not the right fusiform, showed priming on both the similar and the dissimilar conditions (figure 1). In separate contrasts, priming with similar letters was

significant in the left fusiform gyrus (67 voxels) and the left parietal cortex (21 voxels), and fell short of significance in the right fusiform gyrus (8 voxels, p=0.066). With dissimilar letters, priming reached significance in the left fusiform gyrus only (coordinates -44, -56, -12; 10 voxels). The interaction of word repetition with letter similarity never reached significance, however, even in the right fusiform gyrus (t=0.93, n.s.). Thus, the results indicate case invariance in the left fusiform gyrus, and merely suggest, but do not prove, that the right fusiform may be sensitive to visual similarity rather than to genuine case invariance.

Letter binding and invariance for letter position. Experiment 2 used a 3x2 design with prime type (same word, anagram, or different word), and retinal location (same or different) as factors (figure 2). An ANOVA on median RTs revealed a main effect of prime type ($F(2,30)=5.67$, $p=0.008$). The same-word condition was 9 ms faster than the anagram condition ($F(1,15)=6.82$, $p=0.020$) and 11 ms faster than the different-word condition ($F(1,15)=10.4$, $p=0.006$). The latter conditions did not differ ($F<1$). There was no effect or interaction involving location (all $Fs<1$). In particular, repetition priming remained significant when the retinal locations of the prime and target were shifted by one letter (12 ms effect, $F(1,15)=5.26$, $p=0.037$). Conversely, there was no priming between a word and its anagram, even when most letters were presented at the same retinal location (4 ms effect, $F<1$). Thus, behavioral priming depended exclusively on a location-invariant representation of the whole word.

FMRI, however, revealed a subdivision of the VWFA into at least two subareas (figure 2, table 1). First, in the left and right posterior fusiform, activation was reduced only in two conditions: when the same word was presented at the same location, or when an anagram was presented at a location shifted by one letter position. Those are the only cases in which the same letters were repeated at the same retinal location. Thus, those regions may comprise

"letter detectors" tuned the presence of a given letter at a specific retinal location (Peressotti & Grainger, 1995).

Second, more anteriorily in the middle fusiform gyrus, activation was reduced whenever the same word was presented twice, even when shifted by one letter location. This suggested that location-invariance was achieved in this region. Location-invariant priming was observed mainly in the left fusiform gyrus, while the right homolog region showed a mixture of location-specific and location-invariant responses within the same voxel (figure 2C, right column).

To confirm that the left posterior and middle fusiform were functionally different, we extracted their peak activation relative to baseline and submitted them to an ANOVA with factors of region and conditions (5 levels; see fMRI Methods). There was indeed a significant condition X region interaction ($F(4,60)=3.15$, $p=0.020$). Targeted contrasts revealed location-specific letter priming in the posterior ($F(1,15)=8.00$, $p=0.013$) but not the middle fusiform ($F<1$), and location-invariant word priming in the anterior ($F(1,15)=6.32$, $p=0.024$) but not the posterior fusiform ($F<1$).

Finally, there was some suggestion of another more anterior subdivision. Within the location-invariant region, the middle portion of the left fusiform gyrus (y=-56) showed identical priming in the same-word and anagram conditions. This suggests that only fragments of the words, common to the words and their anagrams, were coded at this level. However, the more anterior subpeak of this cluster showed more priming for same-words than for anagrams ($F(1,15)=4.92$, $p=0.042$). This paralleled response times and suggested that whole-word coding was beginning to emerge at that stage. This result should be interpreted cautiously, however, because the condition X region interaction failed to reach significance ($F<1$) when middle and anterior fusiform activations were entered into a common ANOVA.

Discussion

The present findings demonstrate the potential of joint behavioral and neuroimaging priming studies for the dissection of stages of processing. Our previous work (Dehaene et al., 2001) dissociated two levels of word priming: the right occipital cortex was sensitive only to the repetition of the same physical stimuli, suggesting a coding of low-level visual features, while an extended strip of left ventral occipito-temporal cortex showed cross-case priming, suggesting a more abstract coding. The present results clarify the contribution of this region to word recognition. Experiment 1 indicates that this region is not merely coding for the visual similarity of upper and lowercase words. Rather, it encodes the arbitrary mapping between upper and lowercase letters. Furthermore, experiment 2 shows that this region can be decomposed into at least two smaller subareas. The posterior subpart, observed bilaterally, is not invariant for location: it shows priming only when the same letters are presented at the same retinal location. Thus, this region may contain the location-specific letter detectors postulated by some psychological models (Peressotti & Grainger, 1995). Conversely, we found priming across retinal locations in the middle fusiform gyrus, mostly in the left hemisphere. The suggestion that this area holds a location-invariant representation of words fits with previous fMRI and ERP studies, which indicate that words presented to the left or right hemifield, although initially processed in distinct retinotopic visual areas, eventually converge towards the left occipito-temporal region (Cohen et al., 2000; Cohen et al., 2002; McCandliss, Curran, & Posner, 1993).

Here, we only tested invariance for a shift of one letter position. Nevertheless, computationally, this already raises an invariance problem, because it changes radically the pattern of brain activity in early visual areas. The logic of the priming method suggests that the left middle fusiform region may contain neurons that recognize the same word regardless of small position changes, and that invariance is attained in a series of stages, with a case-

invariant but location-specific representation of letters preceding a more globally invariant code.

Our results tentatively suggest a further antero-posterior subdivision within this location-invariant region. Most of this region shows identical priming to repeated words and to anagrams, but the most anterior voxels showed more priming for words than for anagrams. Unfortunately, severe signal drop-off due to susceptibility artifacts in fMRI prevented us from pursuing priming effects more anteriorily in the ventral temporal cortex. The behavioral results, however, clearly showed priming sensitive exclusively to whole words, not their component letters. This implies that a whole-word level of coding must exist and can be activated by subliminal masked primes. The anterior fusiform region, which responds cross-modally to words, is a plausible candidate for the source of this whole-word priming effect (Büchel, Price, & Friston, 1998; Nobre et al., 1994).

A possible interpretation of the observed posteror-to-anterior progression is that neurons in the fusiform region are tuned to progressively larger and more invariant units, from visual features in extrastriate cortex to broader units such as graphemes, syllables, morphemes or even entire words as one moves anteriorily in the fusiform gyrus. A similar posterior-to-anterior gradient is observed in the human ventral pathway when scrambling objects into progressively smaller fragments (Lerner, Hendler, Ben-Bashat, Harel, & Malach, 2001).

Our use of the priming method (Grill-Spector & Malach, 2001; Naccache & Dehaene, 2001) relied on several assumptions. We argued that priming in the left fusiform was due to repetition of the same visual word form, but the prime and target also had the same phonology and the same meaning. In the future, the contribution of phonological and semantic codes could be tested by replicating the present experiments with homonyms or synonyms. Nevertheless, words are unlikely to be coded phonologically or semantically in the middle fusiform gyrus because this region responds only to visual words and is thought to be

prelexical, as demonstrated by its identical response to words and to pronounceable pseusowords (Dehaene et al., 2002). Furthermore, lesion of this region leads to pure alexia, a selective deficit of visual word identification with no semantic or phonological impairment (Leff et al., 2001).

The priming method also supposes that repetition effects in fMRI reflect the local code within a brain area (Grill-Spector & Malach, 2001; Naccache & Dehaene, 2001). However, the fact that the prime and target words are identical might be recognized first in a distant area, perhaps using a phonological or semantic code, and only later retro-propagated to the fusiform gyrus, either activating a case-invariant representation or even several case-specific representations. Although this possibility requires investigation, we consider it unlikely because neurophysiological studies indicate that subliminal masking reduces stimulus-induced activity to a transient bottom-up and prevents the top-down re-entry of information (Lamme, 2003; Lamme, Zipser, & Spekreijse, 2002). Furthermore, we and others (Grill-Spector & Malach, 2001; Vuilleumier, Henson, Driver, & Dolan, 2002) have observed distinct priming effects within a few centimeters in the fusiform gyrus, which is hard to explain if top-down effects were propagating throughout the visual system.

It is indeed noteworthy that a greater variety of forms of priming was observed in fMRI than in response times, which were solely sensitive to an invariant whole-word code. Assuming serially organized stages of processing, response times should have reflected the sum of priming effects evoked at each stage, including a contribution from location-specific letter representations. Response time, being a composite measure of many successive processes, may be inherently less sensitive than fMRI. Alternatively, the processing stage that gets reflected in behavior may depend on task instructions. Indeed, when the task is changed to letter-nonletter classification, behavioral priming is found to depend on a location-dependent single-letter stage (Peressotti & Grainger, 1995). Similarly, when subjects are

submitted to a strong speed pressure in a word classification task, performance depends on word fragments rather than the whole-word level (Abrams & Greenwald, 2000). This suggests that subjects can orient their attention towards a specific processing stage, resulting in an increased influence of that stage on response times. Such task effects may tentatively explain why we observed priming in the left parietal region in experiment 1, but not in experiment 2 nor in our previous work (Dehaene et al., 2001). The letter content judgment used in experiment 1 may have put particular emphasis on this region, which is known to be activated during letter and phoneme monitoring tasks (e.g. Simon, Cohen, Mangin, Bihan, & Dehaene, 2002).

We conclude by considering the implications of our results for subliminal processing. It is of course difficult to establish the complete absence of consciousness of the primes. Nevertheless, we used a very short prime duration (29 ms) and powerful forward and backward geometrical masks. Participants did not report seeing the primes and performed randomly on a forced-choice test. Thus, our findings suggest that advanced processing along the ventral visual pathway is possible in the absence of consciousness. Ventral visual activation to unseen stimuli has now been reported in a variety of paradigms including masking (Dehaene et al., 2001), dichoptic fusion (Moutoussis & Zeki, 2002), and extinction in neglect patients (Rees et al., 2000; Vuilleumier, Armony et al., 2002). Thus, contrary to some proposals (e.g. Bar et al., 2001), fusiform activity is not necessarily associated with conscious awareness.

Finally, a new implication of our results is that the binding of letters into words can be performed subliminally, since behavioral repetition priming was highly sensitive to letter order. This fits with neurophysiological recordings, which reveal a high selectivity of infero-temporal neurons to specific combinations of object parts even in anesthetized monkeys (Tsunoda, Yamane, Nishizaki, & Tanifuji, 2001). Singer (1998) distinguishes two forms of

binding: a rigid binding, achieved by dedicated neurons that have learned to respond to particular combinations, and a transient creation of novel combinations, perhaps mediated by temporal synchrony and more tightly associated with conscious processing. Since words are highly overlearned, our results bear only on the first form of binding and thus contribute to refine, but are not necessarily inconsistent with, the view that higher forms of binding require consciousness (Crick & Koch, 1990).

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Area	# voxels in cluster	cluster-level p value (corrected)	Z value at local maximum	Talairach coordinates		
				x	y	z
EXPERIMENT 1						
main effect of repetition suppression						
left fusiform	65	< 0.00001	4.10	-44	-48	-12
			3.73	-52	-60	-8
			2.57	-44	-72	0
left parietal	24	0.001	3.21	-40	-44	60
			2.41	-36	-48	44
right fusiform	11	0.028	3.85	36	-60	-16
conjunction of repetition effects for similar and dissimilar letters						
left fusiform	34		3.91	-48	-52	-12
left parietal	27		3.18	-40	-48	56
EXPERIMENT 2						
repetition suppression for repeated words at same location (replicating experiment 1)						
left fusiform	12	0.005	3.28	-48	-56	-8
			3.03	-48	-48	-8
right fusiform	8	0.019	4.27	40	-60	-8
repetition suppression for same letters at same location						
left fusiform	13	0.004	3.35	-44	-64	-8
			3.27	-36	-68	-12
right fusiform	7	0.026	3.61	36	-60	-12
conjunction of repetition effects for repeated words at same or different location						
left fusiform	16		4.03	-48	-56	-8
			3.72	-48	-48	-8
right fusiform	7		4.68	40	-60	-8

Table 1. Localization of significant fMRI repetition priming effects

Figure Legends

Figure 1. Behavioral and brain-imaging correlates of case-invariant word recognition. ***A,*** schematic representation of our masking paradigm. ***B,*** response times showed repetition priming independent of the visual similarity of the upper and lowercase letters. ***C,*** statistical maps of the fMRI repetition priming effect superimposed on axial slices of averaged T1-weighted images.

Figure 2. Dissociation of location-dependent and location-invariant stages of word recognition. ***A,*** Experimental design. Using anagrams, we dissociated letter and word repetition at the same or at a different location. The two conditions in which the same letters were presented at the same location are outlined with green rectangles. # signs and rectangles are used for clarity and were not actually presented. ***B,*** response times results, revealing a location-invariant whole-word priming effect. ***C,*** fMRI results showing location-dependent priming in the posterior fusiform gyrus (posterior to y=-60, as indicated by the blue dashed line) and location-independent priming in the middle fusiform gyrus (anterior to y=-60), particularly in the left hemisphere. The most anterior voxels in the left fusiform showed a trend towards greater priming with words than with anagrams, paralleling response times.

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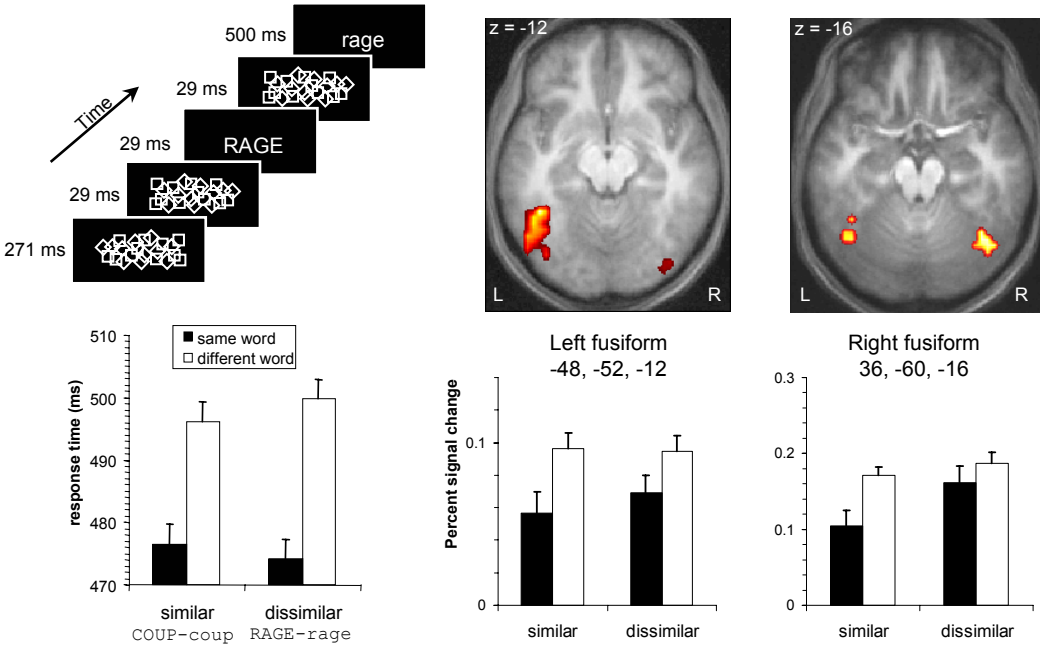
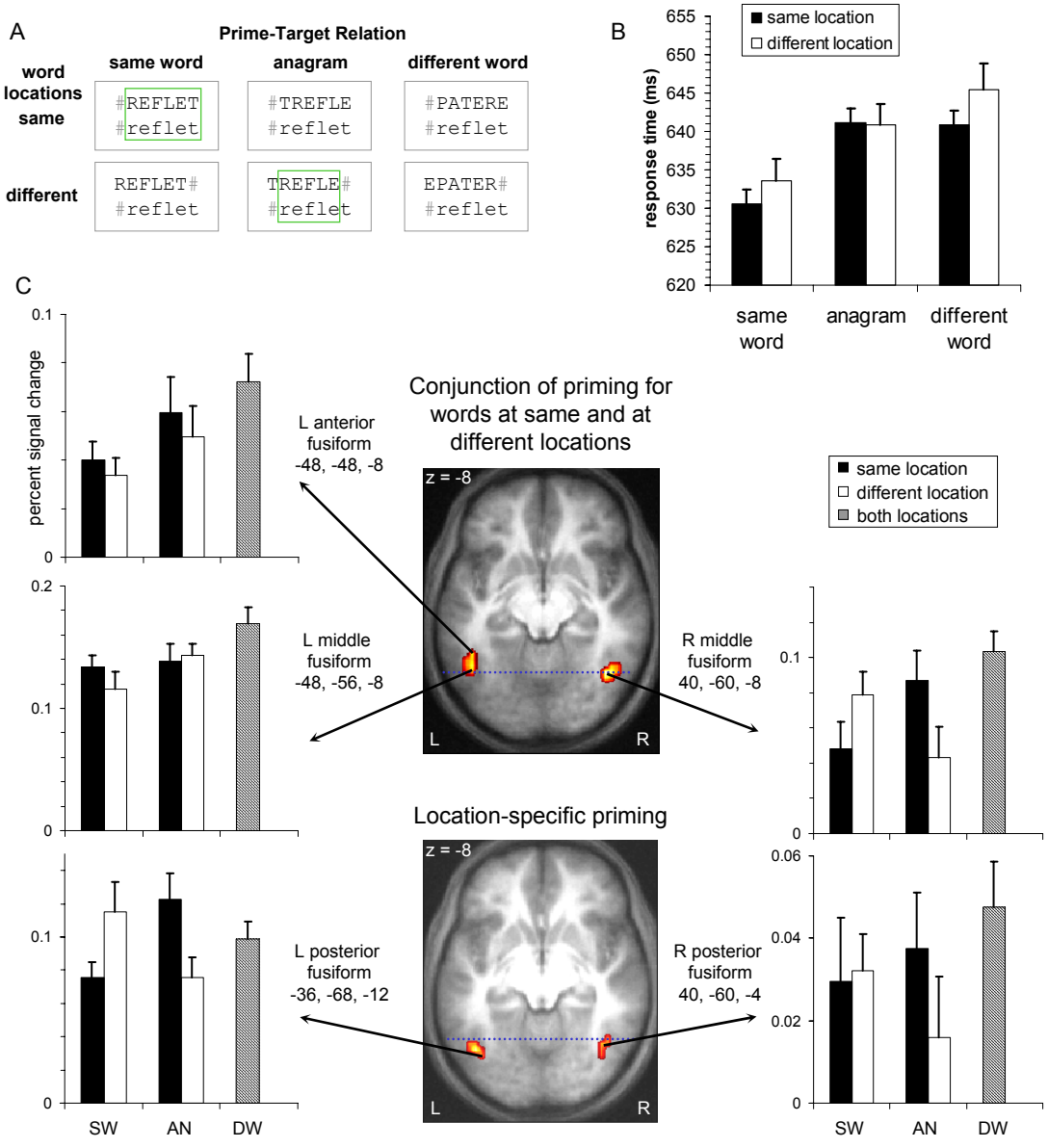


Dehaene et al, Figure 1



Dehaene et al, Figure 2